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AVIAN NEST DENSITIES AND NEST-SITE SELECTION IN FARMSTEAD SHELTERBELTS

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Farmstead shelterbelts are man-made habitats consisting of parallel rows of trees and shrubs designed to protect farmsteads from damaging winds, drifting snow and blowing soil, and to moderate the effects of wind, thereby reducing heat loss from humans, domestic animals, and farm buildings (Smith and Scholten 1980). These habitats may be viewed as small (generally <1 ha) "wooded islands" surrounded by extensive fields of crops, pastures and natural prairies; however, despite their small size and isolation from other wooded habitats, shelterbelts are a source of food and song perches as well as roosting and nesting sites for a number of bird species (Orendurff 1941, Martin 1978). Avian communities in shelterbelts have been examined during the breeding season (Weiser and Hlavinka 1956; Cassel et al. 1966, 1967; Emmerich 1978; Martin 1978). However, with the exception of studies dealing with Mourning Doves (*Zenaida macroura*) (see Nelson 1976 for review), Ring-necked Pheasants (*Phasianus colchicus*) (e.g., Olson and Flake 1975) and Ferruginous Hawks (*Buteo regalis*) (Lokemoen and Duebbert 1976), little is known about the nesting ecology of many bird species breeding in shelterbelts. A study by Field (1971) represents the only published report giving the total number of nests per bird species. Her study dealt only with a portion of one shelterbelt where tree/shrub species used and height above ground of 75 nests of four bird species were noted. As part of an investigation of breeding-bird diversity in 69 shelterbelts, Martin (1978) examined 185 nests of eight species and noted tree/shrub species used, height above ground, lateral distance of nest from main stem, and distance of nest from top of tree/shrub. However, his study did not attempt to locate total nests per shelterbelt nor total nests per season.

A determination of both the number of avian species nesting in farmstead shelterbelts and the abundance of nests per species is an initial and important step in assessing whether or not these small, narrow, agricultural habitats are valuable nesting areas or instead perhaps function to attract predators, hence reducing fledging success (see Gates and Gysel 1978). Moreover, because farmstead shelterbelts are restricted in size, the availability of nest-sites conceivably could be a limiting resource to birds. Thus, a knowledge of factors critical to nest-site selection would give a better understanding of how coexisting nesting species effectively exploit these "wooded islands" (after Pianka 1973, Schoener 1974).

In this paper, I examine the suitability of farmstead shelterbelts as nesting habitats for birds by estimating the annual density of total nests per bird species. Further, I quantify patterns of nest-site selection in common nesting bird species based on two components: (1) types of woody species used as nesting substrate and (2) structural characteristics of nest-sites. Results obtained by this study may provide valuable insight into avian nesting requirements so that effective procedures for future planting and maintenance of farmstead shelterbelts can be formulated to benefit nesting avifauna. Such information would be particularly helpful in the intensively-farmed areas of the Great Plains where wooded habitats are at a premium, comprising less than 3% of the total area in this region (Griffith 1976).

STUDY AREA AND METHODS

The study was conducted at the University of Minnesota's Rosemount Agricultural Experiment Station, Dakota Co., Minnesota. Seven shelterbelts were studied ranging in size from 0.21–0.79 ha and in age from 4–33 years. The number of rows of trees and shrubs per shelterbelt varied from 3–9; 30 species of coniferous and deciduous trees and shrubs were planted by landowners. Shelterbelts and land-use practices of the Experiment Station are representative of those in this agricultural region.

Active and inactive nests were located by systematically searching the ground level and all trees and shrubs in each shelterbelt; searches were conducted at least once per week from late June to late September in 1978 and from early March to late September in 1979. If eggs or young were found in a nest that was known to have been constructed earlier in the year (beginning after late March) and subsequently either abandoned or used to rear young by the same or different species, the nest was considered as another nest. Thus, a nest (or nest-site) is defined to include new nests, nests used for renesting, and those used by one species but constructed by another. Nests were often detected by observations of the activities of breeding adults.

Nests constructed prior to the 1978 breeding season were not considered in the analyses and could be distinguished easily from nests of the 1978 breeding season by degree of deterioration occurring over the previous winter. Because the study did not begin until June 1978, nearly 80% of the nests found this year were no longer in use. Species that had built nests subsequently abandoned ("inactive") were determined (estimated 95% accuracy) by the design of the nest or by the presence of shell fragments and/or feathers in the nest (Harrison 1975). The identity of nests positioned higher than 2.5 m above ground was resolved by using 7 × 35 field glasses at ground level, by climbing to the height of the nest, or by inspection with a mirror and pole device (Parker 1972). The tree and shrub used as a nesting substrate was recorded for each active and inactive nest positioned above ground level; nests on the ground were noted. In addition, 11 structural characteristics of each active and inactive nest above ground level were measured (Table 1).

Densities of nests were computed each year per individual bird species, individual shelterbelt, total bird species and total shelterbelts. I believe that virtually all nests in 1979 were located and correctly identified. However, because the 1978 search of nests began in June, an unknown fraction of the total nests constructed in 1978 likely was not found due to destruction by predators or climatic factors. Thus, a comparison of densities between 1978 and 1979 is probably not valid. There also are other problems inherent in comparisons of

Table 1

Abbreviations and Descriptions of 11 Structural Characteristics Measured at Each Active and Inactive Bird Nest Located above Ground Level in Seven Farmstead Shelterbelts in Southern Minnesota in 1978 and 1979

Abbreviation	Description
HTTR	Height (m) of tree or shrub in which the nest was located.
HTNT	Height (m) of the nest above ground.
DICA	Diameter (m) of the canopy of the tree or shrub at the height of the nest above ground.
DITR	Diameter (cm) of the largest woody stem touching and/or supporting the nest; measured at the nest-site.
DINT	Lateral distance (m) of the nest from the main trunk of the tree or shrub containing the nest.
PTGC	Percentage of herbaceous vegetation within a 1-m radius of a point directly below the nest at ground level.
HTGC	Maximum height (cm) of herbaceous vegetation within a 1-m radius of a point directly below the nest at ground level.
STLE	Number of woody stems <2.5 cm in diameter which was within a 1-m radius of the nest but exclusive of the woody stem nearest the nest (see DITR above).
STMO	Number of woody stems ≥2.5 cm in diameter which was within a 1-m radius of the nest but exclusive of the woody stem nearest the nest (see DITR above).
COMP	Compass direction (degrees) of the nest relative to the position of the main trunk of the tree or shrub containing the nest.
CLOS	Extent of closure or conspicuousness of a nest based on the amount of woody and herbaceous vegetation (estimated to the nearest 10%) in an approximate 1-m radius sphere surrounding the nest-site.

nest densities as true of most field studies (see Miller and Johnson 1978). However, I feel that a comparison of approximate densities has value when comparing among bird species or habitats if done with caution (e.g., see Gates and Gysel 1978).

Nest-site selection based on differential use of woody species by all bird species combined (N = 17) or by individual bird species (N = 5 most common bird species) was determined by comparing observed versus expected number of nests per woody species using tests for goodness of fit (Sokal and Rohlf 1969). Ratios of observed to expected numbers of nests of the five common bird species in each shrub or tree ("woody") species were used to arbitrarily rank individual nesting substrates; a ratio ≥1.50 was used to designate a woody species as a preferred substrate. Substrate nesting breadth, NB_{su}, or the degree of ecological specialization in selection of woody species for nest-sites, was derived for each of the five common bird species. NB_{su} was based on actual availability of each woody species in the seven shelterbelts and was obtained by the equation:

$$NB_{su} = (\lambda i)^{1/N_i}$$

and

$$\log \lambda_i = (\Sigma\, p_{ij} \log q_j - \Sigma\, p_{ij} \log p_{ij})(N_i).$$

For bird species i, N_i is the total number of nests, p_{ij} is the proportion of observed nests in the j^{th} woody species and q_j is the proportion of expected nests in the j^{th} woody species. Values of NB_{su} could range from 0–1, with 1 indicating maximum generality in use of different woody species as nesting substrates (see Petraitis 1979). Substrate nesting overlap, NO_{su}, was calculated between pairs of the five common bird species by the sum of the proportions of nests in common by a pair that were located in each of the woody species (modified from Yeaton 1974).

Nest-site selection based on the 11 structural characteristics of each nest-site (Table 1) was examined by stepwise discriminant analysis (BMDP7M, Dixon and Brown 1979), where $g = 5$ groups (common bird species), $P = 11$ variables (structural characteristics, Table 1), and $N = 589$ cases (total nests of the five common bird species) in the data matrix. Discriminant analysis is an appropriate multivariate statistical technique to detect differences in microhabitat use among species (see Dueser and Shugart 1978, 1979). *A priori* probability of membership for each case in a group was based on the proportion of total cases represented in that group. Normality and homogeneity of variances for the variables were ensured by appropriate transformations (Green 1979, Johnson 1981), and each were tested by graphical plots of observations or by F_{max}-tests, respectively (Sokal and Rohlf 1969, Johnson 1981). Characteristics were entered into the discriminant functions in decreasing order of their importance in discriminating nest-sites among bird species (after Raphael 1981). A characteristic was excluded from entry if the F-to-enter (statistic computed at each step from a single-classification analysis of covariance where covariates are previously entered characteristics) did not exceed the F-to-remove (statistic obtained for the characteristic using a single-classification ANOVA before entering any characteristic into the function) (Dixon and Brown 1979). An approximate F-statistic based on transformation of Wilks' Λ was used to test for overall differences among group means based on the characteristics entered into the discriminant function; F values computed from Mahalanobis D^2 statistics tested between each pair of group means (Lachenbruch 1975:25, Dixon and Brown 1979). Eigenvalues, discriminating information and group means of orthogonal canonical variables (linear combinations of structural characteristics) were derived from between-group and within-group covariance matrices. The canonical variables were adjusted so that the (pooled) within-group variances were 1 and their overall mean was 0; the canonical variables then were evaluated at group means (Dixon and Brown 1979). The significance of discrimination afforded by each of the canonical variables (discriminant functions) was tested using Bartlett's χ^2 approximation tests based on Wilks' Λ criterion computed as a function of the eigenvalues (Cooley and Lohnes 1971:249). A jackknifed validation procedure was used to reduce the bias of group classifications (each case is classified into a group based on a classification function which includes all cases except the one being classified [Dixon and Brown 1979]).

For each individual case (nest), Mahalanobis D^2 was derived as the distance to each group (species) mean. These distances were used to calculate a mean Mahalanobis D^2 for each of the five common bird species. Structural nesting breadth, NB_{st}, then was estimated by obtaining a coefficient of variation based on mean values of Mahalanobis D^2 for each of the five species (modified from Dueser and Shugart 1979). The coefficient of variation is a proper measure of variation when comparing sample means that are known to be statistically different (Sokal and Rohlf 1969) and can be an approximation of breadth in resource use when using discriminant analysis (Dueser and Shugart 1979). Structural nesting overlap, NO_{st}, of the five common bird species was determined by a plot of the two principal canonical variables (Lachenbruch 1975) and the principal axes technique (see Sokal and Rohlf 1969, Dueser and Shugart 1979, Williams 1981). A plot of 95% confidence ellipses for species' cases was made rather than a plot using ellipses for species means. NO_{st} between two species then was computed as the ratio of the area of overlap for the two species relative to the cumulative

area, for that pair of species (after Dueser and Shugart 1979). Thus, NB_{st} was obtained by simultaneously considering all canonical variables extracted, whereas NO_{st} was based only on the two canonical variables giving the most discriminating information among bird species.

RESULTS

Nest densities.—A total of 617 nests was found in seven shelterbelts; 272 (81.9 nests/ha) in 1978 and 345 (103.9 nests/ha) in 1979 (Table 2). Densities of nests among individual shelterbelts in both years averaged 88.5 nests/ha and ranged from 28.8 nests/ha in a three-row, 5-year-old coniferous shelterbelt in 1978 to 186.4 nests/ha in a five-row, 32-year-old coniferous-deciduous shelterbelt in 1979.

Nine of 17 bird species nested in the shelterbelts in both 1978 and 1979, whereas eight additional species nested in either 1978 or 1979 only (Table 2). Nests of Common Grackle (*Quiscalus quiscula*), Mourning Dove, American Robin (*Turdus migratorius*), Gray Catbird (*Dumatella carolinensis*) and Chipping Sparrow (*Spizella passerina*) comprised 95.5% (N = 589) of the total number of nests found in both years combined. Variation in density of nests among individual shelterbelts within or between years often was attributed to the presence of large numbers of grackles. For example, density of grackle nests nearly doubled from 1978 (36.4 nests/ha) to 1979 (64.5 nests/ha); nests of this species occurred in all shelterbelts in 1979 versus five of seven shelterbelts in 1978. Ring-necked Pheasant, Downy Woodpecker (*Picoides pubescens*), Barn Swallow (*Hirundo rustica*), Black-capped Chickadee (*Parus atricapillus*), American Goldfinch (*Carduelis tristis*) and Vesper Sparrow (*Pooecetes gramineus*) were observed in one or more shelterbelts during the breeding season of both years (see Yahner 1980a) but nested in other habitats at the Rosemount Station.

Selection of substrate.—A total of 3589 woody plants of 31 species was available as substrate for nests in the seven shelterbelts (Table 3). Numbers of observed nests for all bird species combined were considerably different from those expected in several abundant ($N > 30$ individual plants) coniferous and deciduous species ($P < 0.001$). Preferred coniferous species included Colorado blue spruce (*Picea pungens*), white spruce (*P. glauca*) and Black Hills spruce (*P. g. densata*), whereas infrequently used conifers were white cedar (*Thuja occidentalis*), red pine (*Pinus resinosa*) and Douglas fir (*Pseudotsuga menziesii*). Deciduous species favored for nest-sites were eastern cottonwood (*Populus deltoides*), silver maple (*Acer saccharinum*) and box elder (*A. negundo*). Fewer nests than expected were found in various deciduous trees and shrubs, such as green ash (*Fraxinus pennsylvanica*), caragana (*Caragana arborescens*) and amur maple (*A. ginnala*). In contrast, numbers of observed compared to expected nests were nearly equal in ponderosa pine (*P. ponderosa*) and tartarian

Table 2

Total Number of Nests, Proportion (%) of Total Nests and Density (no./ha) of Total Nests of 17 Bird Species in Seven Farmstead Shelterbelts (3.32 ha) in Southern Minnesota in 1978, 1979 and Both Years Combined

Bird species	Total no. nests			Proportion total nests			Density total nests		
	1978	1979	both	1978	1979	both	1978	1979	both
Common Grackle (*Quiscalus quiscula*)	121	214	335	44.5	62.0	54.3	36.4	64.5	50.5
Mourning Dove (*Zenaida macroura*)	62	74	136	22.8	21.4	22.0	18.7	22.3	20.5
American Robin (*Turdus migratorius*)	54	33	87	19.9	9.6	14.1	16.3	9.9	13.1
Gray Catbird (*Dumetella carolinensis*)	12	5	17	4.4	1.5	2.8	3.6	1.5	2.6
Chipping Sparrow (*Spizella passerina*)	8	6	14	2.9	1.7	2.3	2.4	1.8	2.1
Brown Thrasher (*Toxostoma rufum*)	1	4	5	0.4	1.2	0.8	0.3	1.2	0.8
Common Crow (*Corvus brachyrhynchos*)	4	0	4	1.5	0.0	0.6	1.2	0.0	0.6
Song Sparrow (*Melospiza melodia*)	2	2	4	0.7	0.6	0.6	0.6	0.6	0.6
Blue Jay (*Cyanocitta cristata*)	2	1	3	0.7	0.3	0.5	0.6	0.3	0.5
Red-winged Blackbird (*Agelaius phoeniceus*)	3	0	3	1.1	0.0	0.5	0.9	0.0	0.5
Eastern Kingbird (*Tyrannus tyrannus*)	1	1	2	0.4	0.3	0.3	0.3	0.3	0.3
Indigo Bunting (*Passerina cyanea*)	2	0	2	0.7	0.0	0.3	0.6	0.0	0.3
Great Horned Owl (*Bubo virginianus*)	0	1	1	0.0	0.3	0.2	0.0	0.3	0.2
Starling (*Sturnus vulgaris*)	0	1	1	0.0	0.3	0.2	0.0	0.3	0.2
Common Yellowthroat (*Geothlypis trichas*)	0	1	1	0.0	0.3	0.2	0.0	0.3	0.2
House Sparrow (*Passer domesticus*)	0	1	1	0.0	0.3	0.2	0.0	0.3	0.2
Eastern Meadowlark (*Sturnella magna*)	0	1	1	0.0	0.3	0.2	0.0	0.3	0.2
Total	272	345	617				81.9	103.9	93.4

Table 3

Abundance of and Use of 31 Woody Species as Nesting Substrate by 17 Bird Species in Seven Farmstead Shelterbelts (3.32 ha) in Southern Minnesota in 1978 and 1979

Woody species	Total no. plants	Observed no. nests	Expected no. nests[a]	Proportion total observed nests
Colorado blue spruce (*Picea pungens*)	113	125	19.4	20.3
White spruce (*Picea glauca*)	242	124	41.6	20.1
Cottonwood (*Populus deltoides*)	201	60	34.6	9.9
Silver maple (*Acer saccharinum*)	197	50	33.9	8.1
Ponderosa pine (*Pinus ponderosa*)	220	38	37.8	6.6
Box elder (*Acer negundo*)	33	35	5.7	5.7
Black Hills spruce (*Picea glauca densata*)	37	30	6.4	4.9
Green ash (*Fraxinus pennsylvanica*)	421	20	72.4	3.2
Tartarian honeysuckle (*Lonicera tatarica*)	111	19	19.1	3.1
White cedar (*Thuja occidentalis*)	195	16	33.5	2.6
Jack pine (*Pinus banksiana*)	72	14	12.4	2.3
Caragana (*Caragana arborescens*)	423	13	72.7	2.1
Amur maple (*Acer ginnala*)	153	12	26.3	1.9
Norway spruce (*Picea abies*)	88	11	15.1	1.8
Red pine (*Pinus resinosa*)	171	10	29.4	1.6
American elm (*Ulmus americana*)	112	9	19.3	1.5
Ural willow (*Salix purpurea*)	220	5	37.8	0.8
Buffalo berry (*Shepherdia argentea*)	17	4	2.9	0.6
Flowering crab (*Malus floribunda*)	7	3	1.2	0.5
Common lilac (*Syringa vulgaris*)	251	3	43.2	0.5
Russian olive (*Elaeagnus angustifolia*)	25	2	4.3	0.3
Red-berried elder (*Sambucus pubens*)[b]	10	2	1.7	0.3
High-bush cranberry (*Viburnum trilobum*)	9	2	1.5	0.3
River birch (*Betula nigra*)	1	1	0.2	0.2
Honey locust (*Gleditsia tricancanthos*)	99	1	17.0	0.2
Chokecherry (*Prunus virginiana*)	11	1	1.9	0.2
Southern arrowwood (*Viburnum dentatum*)	24	1	4.1	0.2
Gray dogwood (*Cornus racemosa*)	18	0	3.1	0.0
Red-osier dogwood (*Cornus stolonifera*)	10	0	1.7	0.0
Laurel-leaved willow (*Salix pentandra*)	9	0	1.5	0.0
Douglas fir (*Pseudotsuga menziesii*)	89	0	15.3	0.0
Miscellaneous[c]	—	6	—	1.0
Total	3589	617	—	—

[a] Expected number of nests was determined from the total number of plants and the total number of observed nests. Expected number of nests is significantly different from observed number of nests ($\chi^2 = 1227$, df = 30, $P < 0.001$. Test for goodness of fit, Sokal and Rohlf (1969).

[b] Woody species which colonized shelterbelts.

[c] Refers to nests found on ground or in log and brush piles.

Table 4

Total Number of Observed Nests (and Expected Nests) of Five Common Bird Species in 26 Woody Species Used as Nesting Substrate in Seven Farmstead Shelterbelts in Southern Minnesota in 1978 and 1979

Woody species[a]	Total number of nests/bird species[b]				
	Common Grackle	Mourning Dove	American Robin	Gray Catbird	Chipping Sparrow
Colorado blue spruce	57 (10.55)[2]	35 (4.28)[1]	25 (2.74)[2]	1 (0.54)[7]	8 (0.44)[1]
White spruce	56 (22.59)[5]	48 (9.17)[3]	19 (5.87)[6]	0 (1.15)	0 (0.94)
Cottonwood	50 (18.76)[4]	8 (7.62)	3 (4.87)	0 (0.95)	0 (0.78)
Silver maple	40 (18.39)[6]	5 (7.47)	4 (4.78)	0 (0.93)	0 (0.77)
Ponderosa pine	37 (20.53)[7]	0 (8.34)	1 (5.33)	0 (1.04)	0 (0.86)
Box elder	29 (3.08)[1]	0 (1.25)	4 (0.80)[4]	0 (0.16)	0 (0.13)
Black Hills spruce	11 (3.45)[3]	9 (1.40)[2]	8 (0.90)[3]	1 (0.18)[5]	1 (0.14)[2]
Green ash	10 (39.30)	4 (15.95)	6 (10.21)	0 (1.99)	0 (1.64)
Tartarian honeysuckle	0 (10.36)	3 (4.21)	2 (2.70)	8 (0.53)[4]	3 (0.43)[3]
White cedar	7 (18.20)	3 (7.39)	5 (4.73)	0 (0.92)	0 (0.76)
Jack pine	7 (6.72)	4 (2.73)	0 (1.75)	0 (0.34)	0 (0.28)
Caragana	12 (39.48)	0 (16.03)	0 (10.25)	0 (2.00)	0 (1.65)
Amur maple	0 (14.28)	10 (5.80)[4]	2 (3.71)	0 (0.72)	0 (0.60)
Norway spruce	4 (8.21)	0 (3.33)	4 (2.13)[7]	0 (0.42)	2 (0.34)[4]
Red pine	9 (15.96)	0 (6.48)	0 (4.15)	0 (0.81)	0 (0.67)
American elm	3 (10.45)	1 (4.24)	1 (2.71)	1 (0.53)[6]	0 (0.44)
Ural willow	0 (20.53)	2 (8.34)	0 (5.33)	0 (1.04)	0 (0.86)
Buffalo berry	0 (1.59)	1 (0.64)	0 (0.41)	2 (0.08)[2]	0 (0.07)
Flowering crab	1 (0.65)	0 (0.27)	2 (0.17)[1]	0 (0.03)	0 (0.03)
Common lilac	2 (23.42)	0 (9.51)	0 (6.08)	1 (1.19)	0 (0.98)
Russian olive	0 (2.33)	1 (0.95)	1 (0.61)	0 (0.12)	0 (0.10)
Red-berried elder	0 (0.93)	0 (0.38)	0 (0.24)	2 (0.05)[1]	0 (0.01)
High-bush cranberry	0 (0.84)	0 (0.34)	0 (0.22)	1 (0.04)[3]	0 (0.04)
River birch	0 (0.09)	1 (0.04)	0 (0.02)	0 (0.00)	0 (0.00)
Honey locust	0 (9.24)	1 (3.75)	0 (2.40)	0 (0.47)	0 (0.39)
Chokecherry	0 (1.02)	0 (0.42)	1 (0.27)[5]	0 (0.05)	0 (0.04)
No. woody species used	16	16	16	8	4
Total no. observed nests	335	136	87	17	14
G-statistics[c]	782	314	174	35	39
Level of significance	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P > 0.10$	$P > 0.01$
Substrate nesting breadth, NB_{su}[d]	0.44	0.31	0.31	0.09	0.08

[a] Scientific names of woody species and total number of individual plants for each are given in Table 3. Woody species not used by at least one of five common bird species are excluded from table.

[b] Rank of each woody species as nesting substrate per bird species is based on the ratio of observed to expected number of nests. The greater the ratio, the higher the rank as indicated by a lower numeric subscript. A ratio ≥ 1.50 arbitrarily designated a preference as a nesting substrate; a ratio <1.50 was excluded from ranking.

[c] Comparison of observed to expected numbers of nests per bird species (df = 30). Test for goodness of fit, Sokal and Rohlf (1969).

[d] See text for derivation.

TABLE 5

SUBSTRATE NESTING OVERLAP, NO_{SU}, BETWEEN PAIRS OF FIVE COMMON BIRD SPECIES NESTING IN SEVEN FARMSTEAD SHELTERBELTS IN SOUTHERN MINNESOTA IN 1978 AND 1979

Bird species pair	NO_{su} (%)[a]
Common Grackle—Mourning Dove	55
Common Grackle—American Robin	59
Common Grackle—Gray Catbird	11
Common Grackle—Chipping Sparrow	22
Mourning Dove—American Robin	78
Mourning Dove—Gray Catbird	15
Mourning Dove—Chipping Sparrow	35
American Robin—Gray Catbird	15
American Robin—Chipping Sparrow	43
Gray Catbird—Chipping Sparrow	33

[a] NO_{su} (%) is calculated as the sum of proportions of nests (Table 4) in common by a pair in each woody species used as a nesting substrate.

honeysuckle (*Lonicera tatarica*). Three of the five common nesting bird species showed a significant difference ($P < 0.001$) in observed versus expected use of nesting substrate (Table 4). All five common bird species preferred spruces (*Picea* spp.), yet each also displayed specific preferences for other woody species.

The five common bird species varied in substrate nesting breadth, NB_{su} (Table 4). NB_{su} was highest in grackles, intermediate in doves and robins, and lowest in catbirds and sparrows. The greatest amount of substrate nesting overlap, NO_{su}, occurred with doves and robins (78%, Table 5). These two species exhibited similar NO_{su} with grackles (55–59%). In contrast, catbirds had little joint use of nesting substrate with doves (15%), robins (15%) and grackles (11%). NO_{su} between sparrows and each of the four other species ranged from 22–43%.

Selection of structural characteristics.—Stepwise discriminant analysis based on 11 structural characteristics (Table 1) measured at nest-sites (N = 589) indicated that group means among the five common bird species were not equal ($F = 25.11$; df = 32, 2129; $P < 0.001$). In addition, the group mean of each bird species was significantly different from those of the other species in paired comparisons (F's = 3.73–53.78; df's = 8, 22–462; P's < 0.001). Segregation of nest-sites in discriminant space (after Dueser and Shugart 1979, Raphael 1981) was due only to 8 of 11 structural characteristics (Table 6); of the 11 characteristics, HTTR, DITR and COMP (see Table 1 for abbreviations and descriptions) were not selected for entry into the discriminant function equations. The percentage of total

Table 6

Means and Standard Deviations of 11 Structural Characteristics Measured at Nest-sites of Five Common Bird Species Nesting in Seven Farmstead Shelterbelts in Southern Minnesota in 1978 and 1979

Characteristic[b]	Common Grackle (N = 335)	Mourning Dove (N = 136)	American Robin (N = 87)	Gray Catbird (N = 17)	Chipping Sparrow (N = 14)
HTNT*	6.27 ± 3.51^{drcs}	2.26 ± 1.40^{g}	2.46 ± 1.88^{g}	1.26 ± 0.64^{g}	1.08 ± 0.66^{g}
DICA*	2.43 ± 1.79^{drc}	3.15 ± 1.14^{g}	2.93 ± 1.57^{g}	3.01 ± 1.18^{g}	2.74 ± 1.33
DINT*	0.23 ± 0.62^{ds}	0.51 ± 0.62^{grc}	0.27 ± 0.50^{dcs}	0.12 ± 0.30^{drs}	0.63 ± 0.66^{grc}
HTGC*	0.30 ± 0.32^{drcs}	0.39 ± 0.35^{gcs}	0.39 ± 0.35^{gcs}	1.05 ± 0.78^{gdrs}	0.60 ± 0.54^{gdrc}
PTGC*	44.8 ± 38.3^{rcs}	47.6 ± 36.2^{rcs}	64.3 ± 37.9^{gd}	77.9 ± 32.2^{gd}	79.3 ± 30.8^{gd}
STLE*	0.36 ± 1.98^{cs}	0.65 ± 2.09^{cs}	0.31 ± 1.41^{cs}	9.88 ± 5.55^{gdrs}	2.79 ± 4.97^{gdrc}
STMO*	0.14 ± 0.74^{c}	0.15 ± 0.58^{c}	0.16 ± 0.57^{c}	0.53 ± 0.62^{gdrs}	0.07 ± 0.27^{c}
CLOS*	39.3 ± 27.8^{drcs}	56.6 ± 26.2^{grcs}	63.7 ± 25.1^{gdcs}	96.5 ± 4.9^{gdr}	94.2 ± 5.4^{gdr}
HTTR*^{n}	10.07 ± 5.48^{drcs}	7.16 ± 3.81^{gcs}	6.92 ± 4.29^{gc}	3.34 ± 1.84^{gdr}	4.26 ± 2.87^{gd}
DITR*^{n}	0.08 ± 0.06^{drcs}	0.05 ± 0.05^{gr}	0.06 ± 0.04^{gdcs}	0.03 ± 0.03^{gr}	0.02 ± 0.02^{gr}
COMP^{n}	218.7 ± 100.8	228.6 ± 88.2	225.9 ± 76.5	233.1 ± 84.6	225.0 ± 58.5

[a] N = 589.

[b] Characteristics are listed in order of decreasing importance in discriminating among bird species in stepwise discriminant function. Characteristics indicated by an asterisk are significantly different among species ($P < 0.05$, single-classification ANOVA, Sokal and Rohlf [1969]); superscript n indicates not included in the discriminant function equations (see text). Superscripts, g, d, r, c and s indicate that a mean for a particular characteristic is different ($P < 0.05$, Student-Newman-Keuls test) from mean of Common Grackle, Mourning Dove, American Robin, Gray Catbird, or Chipping Sparrow, respectively. Descriptions and abbreviations of characteristics are from Table 1.

nest-sites accurately classified to bird species averaged 51.1% and ranged from 0.0% in sparrows to 88.1% in grackles (Table 7).

Stepwise discriminant analysis extracted four canonical variables (CV) or linear combinations of the 11 structural characteristics measured at

Table 7

Jackknifed Classification Matrix Giving the Percentage of Nests Correctly Classified to Bird Species and the Numbers of Nests Categorized into Each of the Five Common Bird Species Based on 11 Structural Characteristics Measured at 589 Nest-sites

Bird species	Percentage correct	Number of nests classified/bird species				
		Common Grackle	Mourning Dove	American Robin	Gray Catbird	Chipping Sparrow
Common Grackle	88.1	295	19	17	4	0
Mourning Dove	62.5	28	85	18	5	0
American Robin	34.5	22	33	30	2	0
Gray Catbird	70.6	2	1	2	12	0
Chipping Sparrow	0.0	0	4	7	3	0
Total	—	347	142	74	26	0

TABLE 8

EIGENVALUES, DISCRIMINATING INFORMATION, GROUP (BIRD SPECIES) CANONICAL CORRELATION COEFFICIENTS AND STANDARDIZED COEFFICIENTS OF EIGHT STRUCTURAL CHARACTERISTICS FOR CANONICAL VARIABLES 1 AND 2 EXTRACTED FROM STEPWISE DISCRIMINANT ANALYSIS OF BETWEEN-SPECIES AND WITHIN-SPECIES COVARIANCE MATRICES OF 11 STRUCTURAL CHARACTERISTICS MEASURED AT NEST-SITES (N = 589) OF FIVE COMMON BIRD SPECIES

	Canonical variable[a]	
	1	2
Eigenvalue	1.038	0.474
Percentage of discriminating information	65.1	29.7
Bird species		
Common Grackle	−0.75	−0.30
Mourning Dove	0.71	0.67
American Robin	0.72	0.69
Gray Catbird	3.73	−2.90
Chipping Sparrow	2.17	−0.02
Structural characteristic[b]		
HTNT	−0.23	−0.25
DICA	0.24	0.12
DINT	0.16	0.29
HTGC	0.75	−0.09
PTGC	0.01	0.00
STLE	0.19	−0.40
STMO	−0.27	0.43
CLOS	0.01	0.00

[a] Canonial variables 1 and 2 are both significant ($P < 0.001$) based on Wilks' Λ criterion computed as a function of the eigenvalues using Bartlett's χ^2 approximation (Cooley and Lohnes 1971:249). Wilks' $\Lambda = 0.31$ and 0.63; $\chi^2 = 685$ and 272; df = 44 and 30, respectively.

[b] Descriptions and abbreviations of structural characteristics are from Table 1. Characteristics not included in discriminant equations (Table 6) are omitted.

nest-sites, which best segregated among the five common bird species. Only CV1 and CV2 afforded a significant ($P < 0.001$) degree of discrimination (Table 8). CV1 is a "herbaceous" variable because it principally includes the structural variable HTGC, although HTNT, DICA and STMO are important also, as indicated by relatively high standardized coefficients (after Raphael 1981, Williams 1981). CV1 accounts for 65.1% of the discriminating information that is available in the 11 characteristics measured at nest-sites to separate bird species. CV2 is termed a "woody stem" variable because it mainly associates the variables STLE and STMO. CV2 explains 29.7% of the discriminating information. CV3 and CV4 are neither biologically interpretable nor statistically significant ($P > 0.05$), and

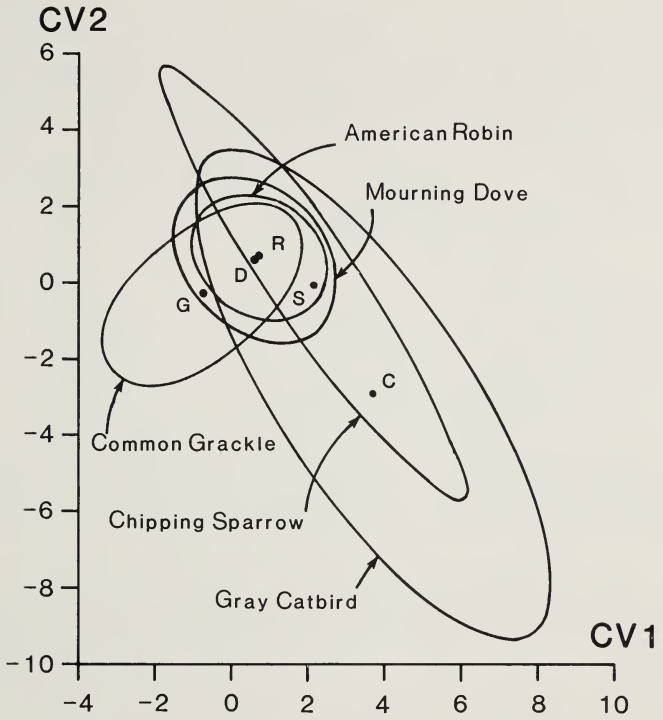

FIG. 1. Plot of group means of bird species for CV1 and CV2 (Table 8) and 95% confidence ellipses for the species' cases (nests) on CV1 and CV2 using the principal axes technique (Sokal and Rohlf 1969, Dueser and Shugart 1979). Group means: G = Common Grackle, D = Mourning Dove, R = American Robin, C = Gray Catbird and S = Chipping Sparrow.

account for only 3.7 and 1.5%, respectively, of the discriminating information.

A plot of the two principal canonical variables, CV1 on CV2 (Fig. 1), gives the best visual and ecologically interpretable illustration of the differences in the structural characteristics of nest-sites among the five common bird species. The relatively narrow, elongated ellipses of grackles, catbirds and sparrows (Fig. 1) indicate that most variance could be explained by CV1 (Table 8) (see Sokal and Rohlf 1969). In contrast, the more circular ellipses of robins and doves suggest that CV1 and CV2 were of nearly equal importance in discriminating nest-sites of these species. Species with group means to the right in Fig. 1 along the "herbaceous" variable, such as the catbird and the sparrow, were characterized by well-hidden nests. Nests of these two species were located close to the ground

TABLE 9

STRUCTURAL NESTING OVERLAP, NO_{ST}, BETWEEN PAIRS OF FIVE COMMON BIRD SPECIES NESTING IN SEVEN FARMSTEAD SHELTERBELTS IN SOUTHERN MINNESOTA IN 1978 AND 1979

Bird species pair	NO_{st} (%)[a]
Common Grackle—Mourning Dove	33
Common Grackle—American Robin	33
Common Grackle—Gray Catbird	9
Common Grackle—Chipping Sparrow	8
Mourning Dove—American Robin	69
Mourning Dove—Gray Catbird	20
Mourning Dove—Chipping Sparrow	26
American Robin—Gray Catbird	14
American Robin—Chipping Sparrow	20
Gray Catbird—Chipping Sparrow	34

[a] NO_{st} is calculated from 95% confidence ellipses for species' cases (nests) on canonical variables 1 and 2 (Fig. 1) by the ratio of the area of overlap for two species relative to the cumulative area for that pair of species (after Dueser and Shugart 1979).

and were well concealed by herbaceous vegetation (Table 6), compared to nests of other species. On the other hand, the mean of the grackle nests was located to the left in Fig. 1 because nests were often high above ground and well exposed. Means of dove and robin nests were intermediate in height above ground and percentage of herbaceous cover.

The position of group means along the "woody stem" variable essentially separates catbird nests from those of the other four species (Fig. 1), based on the density of woody stems surrounding nests (Table 6). Further, catbird and grackle nests tended to be located near the main stem of the nesting substrate relative to the location of nests of the other three species.

Structural nesting breadth, NB_{st}, or the relative variability in the distance of each species' nest from its respective group mean in 4-dimensional hyperspace (corresponding to four canonical variables) was greatest in grackles (NB_{st} = 1.97), followed by those of robins (1.89), sparrows (1.12), doves (1.08) and catbirds (0.89). As with NO_{su} (Table 5), structural nesting overlap, NO_{st}, in 2-dimensional hyperspace (Fig. 1) was greatest between doves and robins (69%, Table 9). NO_{st} of catbirds with sparrows and NO_{st} of grackles with either doves or robins were nearly equal (33–34%). The least amount of shared use of structural characteristics of nestsites was shown between grackles and either catbirds or sparrows (8–9%).

DISCUSSION

Suitability of shelterbelts as nesting habitat.—Farmstead shelterbelts are valuable habitats to avifauna in regions of intensive agriculture in

terms of both numbers of breeding species and density of nests (Table 2). The importance of these "wooded islands" is supported perhaps by comparisons to studies conducted in other types of habitats in the midwest region (e.g., see Skinner 1975, George et al. 1979). Studies of avifauna associated with farmstead shelterbelts report large numbers of nests for certain species, particularly grackle, dove and robin nests (see Randall 1955, LaPointe 1958, Field 1971, Martin 1978). In my study, 50.5, 20.5 and 13.1% of total nests (N = 617) were of these three species, respectively (Table 2).

A variety of factors may contribute to the suitability of farmstead shelterbelts as nesting habitat to different bird species in addition to the availability of preferred nesting substrate (Tables 3 and 4), and/or the microhabitat configuration afforded by the substrate (Tables 6 and 8, Fig. 1). One factor may include the spacing pattern used by landowners in planting trees and shrubs within and between rows of shelterbelts and its concomitant effect on vegetative structure. For example, the distance between permanent trees in rows after thinning may be as much as 5–7 m (see Smith and Scholten 1980). This planting practice probably creates favorable nesting areas for bird species adapted to mixed-breeding habitats, i.e., habitats with relatively open overstory canopies and/or dense cover near the ground for nest-sites (Table 6, Fig. 1) (after Gates and Gysel 1978, Stauffer and Best 1980).

The manner in which landowners maintain shelterbelts may also affect their importance to birds as nesting areas (see Read 1964, Smith and Scholten 1980 for maintenance procedures). For instance, younger shelterbelts (≤5 years) often are mowed to remove undesirable vegetation which compete for moisture with tree and shrub seedlings (George 1943). Mowing of dense undergrowth in a 5-year-old shelterbelt may have enabled an Eastern Meadowlark (*Sturnella magna*) to nest in 1978 (Table 2); meadowlark nests are typically characteristic of open, non-wooded habitats (George et al. 1979). Removal of snags is a practice that likely reduces the suitability of shelterbelts for primary and secondary cavity nesters (see Hardin and Evans 1977, Martin 1978, Stauffer and Best 1980). Although Black-capped Chickadees and Downy Woodpeckers were two cavity-nesting species observed in shelterbelts during spring (Yahner 1980a), neither nested in shelterbelts as a probable consequence of few snags and/or small size of shelterbelts. Two known cavities were present in the seven shelterbelts, and those were used as nest-sites by a House Sparrow (*Passer domesticus*) and a Starling (*Sturnus vulgaris*) in 1979 (Table 2).

The attractiveness of farmstead shelterbelts as nesting habitat to a particular bird species conceivably depends on many factors not considered in this study. Among these are type, quantity and availability of food (after

Franzreb 1978), including food items procured in shelterbelts or in contiguous habitats around farmsteads. For example, the probability of an American Robin selecting a shelterbelt as a nesting area may be contingent not only on the presence of *Picea* as nesting substrate (Table 4) but also on proximity of a preferred foraging area near the nest-site. Perhaps a mowed lawn, used as a foraging site and adjacent to the shelterbelt, contains sufficient food resources that were otherwise unavailable or in low abundance within the shelterbelt for raising a brood of robins. Another factor determining use of shelterbelts may be the ability of a bird species to tolerate disturbances associated with farm operations (after Emlen 1974, Cooke 1980). Shelterbelts are usually planted within 30–35 m of homes and buildings (Smith and Scholten 1980), and the disturbances created by humans, domestic animals and farm machinery may disrupt nesting activities of some species more than others. Two additional factors may be that some shelterbelts are narrower than the minimum width of a habitat required by certain breeding species (Stauffer and Best 1980), or that a less aggressive species benefits by the presence of a coexisting, more aggressive species (e.g., catbird) which effectively defends nesting areas against predation and parasitism (Clark and Robertson 1979). Finally, the presence of mammalian nest predators, such as red squirrels (*Tamiasciurus hudsonicus*), in certain types of shelterbelts (Nelson 1976, Yahner 1980b) may influence the overall suitability of these habitats as nesting areas.

Nest-site selection: substrate and structural considerations.—Farmstead shelterbelts represent an excellent habitat in which to examine patterns of nest-site selection for two reasons. First, the number of suitable nest-sites per bird species is presumably restricted by the limited number of trees and shrubs available (N = 3589 or 1089 plants/ha, this study). Second, nesting substrate among shelterbelts differed with regard to plant species (N = 31) as well as physiognomy.

The five common bird species preferred certain nesting substrate; use of specific woody species for nest-sites was not proportional to the actual number of individual plants per tree or shrub species in the seven shelterbelts (Table 4). These results agree with other studies dealing with doves and grackles (e.g., McClure 1946, LaPointe 1958, Field 1971). Moreover, grackle, dove and robin nests were each found in 16 different woody species (Table 1), but the relative proportions of total nests per woody species were less variable in grackles compared to doves and robins. As a consequence, NB_{su} was highest in the grackle (Table 4). Using NB_{su} as an inverse index of specialization (Levins 1968, Dueser and Shugart 1979) in use of substrate, the grackle may be classified as a generalist or opportunist along a generalist-specialist continuum. At the opposite pole of

the NB_{su} continuum are specialists (low NB_{su}), the catbird and the sparrow. The dove and the robin are positioned toward the middle of the continuum with intermediate values of NB_{su}.

Variability in location of nest-sites, based on structural characteristics (Table 6) and expressed by values of NB_{st}, may be viewed as a generalist-specialist continuum in discriminant 4-space (corresponding to canonical variable 1–4). Again, the grackle, followed by the robin, was less stereotyped in nest-site selection compared to the other three common species. Thus, both measures of nesting breadth were broad in the grackle and the robin but varied from intermediate to narrow with the other species, depending on the measure of breadth. For example, the sparrow was very specific in its choice of nesting substrate ($NB_{su} = 0.08$, Table 4) but was more flexible in selecting the location of nests relative to structural features ($NB_{st} = 1.12$) when compared to the dove or the catbird. Conversely, the dove was capable of using many woody plants ($NB_{su} = 0.31$) yet was stereotypic in terms of structural nesting breadth ($NB_{st} = 1.08$). In short, NB_{su} was not necessarily related to NB_{st} in comparisons within or among common bird species.

Because of the spatially-limited environment of shelterbelts, a certain amount of overlap in both use of specific nesting substrate and structural characteristics surrounding nest-sites is plausible among bird species (after Raphael 1981). NO_{su} and NO_{st} was greatest between doves and robins (Tables 5 and 9), partially the result of the use of robin nests by doves (e.g., McClure 1946, Weeks 1980, pers. obs.). Further, nests of these two species were often indistinguishable (Table 7) on the basis of high NO_{st} (Table 9) and similar mean values for 8 of the 11 structural characteristics (Table 6). On the other extreme, ecological requirements of some species in choice of nest-sites were so different (Tables 4 and 6) that little overlap in substrate use of structural characteristics was expected. For example, NO_{su} and NO_{st} were only 11 and 9%, respectively, between grackles and catbirds (Tables 5 and 9). Only 4 (1.2%) of 335 grackle nests were inaccurately classified as catbird nests (Table 7). Although the group mean of sparrows was segregated from means of each of the other species ($P < 0.001$), all nests ($N = 14$) were classified as being those of dove, robin or catbird (Table 7). This may be partially due to moderate amounts of cumulative overlap by sparrows with these three species in selection of microhabitat for total nest-sites (Table 6 and 9). Alternatively, a structural characteristic(s) not considered in this study may have given better discrimination between nest-sites of sparrows and those of the other three species, perhaps giving better accuracy in classification (see Raphael 1981 for additional discussion). Perhaps sample size was a factor in classification, yet 70.6% of catbird nests ($N = 17$) were categorized accurately (Ta-

ble 7). Yahner (in press) has shown that abundance of this sparrow in both spring and summer is correlated ($P < 0.05$) to the extent of the perimeter of shelterbelts; thus, "edge" of shelterbelts or nesting substrate (NB_{su} = 0.08, Table 4) may be relatively more important than structural features (Table 6) in choice of nest-sites by this species. In short, these small "wooded islands" were sufficiently heterogeneous to allow the five common bird species to select distinct nest-sites (Table 8, Fig. 1), thereby permitting high densities of nests compared to non-wooded habitats in the midwest. If more data were available to quantify patterns of nest-site selection by the 12 other species known to nest in these seven shelterbelts (Table 2), comparisons could be made to test whether or not the five common species were more abundant because of more generalized ecological requirements for nests.

Patterns of nest-site selection: management implications.—A knowledge of patterns of nest-site selection by bird species in shelterbelts may be helpful in formulating effective decisions pertaining to the future design of these farmstead habitats. For instance, based on NB_{su} (Table 4) and NB_{st} the grackle is extremely opportunistic in selection of nest-sites. This species appears capable of exploiting a variety of tree and shrub species (Table 4), with perhaps the only requirement being that the shelterbelt have some tall trees for nest-sites well-above ground level (Table 6, Fig. 1). Because nesting overlap between doves and robins was relatively extensive (Tables 5 and 9), management decisions for the design and the maintenance of shelterbelts may have similar effects on these two species. Stauffer and Best (1980), for example, concluded that partial removal of woody canopy in closed-canopy riparian woodlands would benefit both doves and robins. Thus, the partially-opened canopy that often occurs in farmstead shelterbelts due to spacing and thinning of trees and shrubs likely has similar effects on both of these species. But when spruce (*Picea* spp.), the preferred nesting substrate for doves and robins (Table 4), are planted close together (e.g., 3–4 m), the lower branches typically lose needles if contact is made with contiguous trees or shrubs due to shading (Smith and Scholten 1980). Doves and robins rarely constructed nests in lower (<3 m above ground), defoliated branches of spruce, perhaps because nest-sites of both species required a moderate amount of concealment (Table 6, Fig. 1). Loss of needles in lower branches also can reduce the effectiveness of spruce as wind barriers. Thus, an approximate spacing of 5–6 m between adjacent trees may help retain foliage, thereby serving a dual function of providing a long-term wind barrier and a nesting substrate for two common bird species in shelterbelts (H. Scholten, pers. comm.).

Catbirds, and to some extent sparrows, exhibited relatively narrow nest-

ing breadths and reduced overlap with those of other species (Tables 4, 5 and 9; Fig. 1). Because of stereotypic nest-site selection, an obvious management recommendation is to provide preferred nesting substrate (Table 4). Moreover, nests of these two species (particularly catbirds) were well concealed but close to ground level (Table 6, Fig. 1). Therefore, removal of herbaceous or woody vegetation (i.e., via mowing) should be restricted to areas between rows and attempts should be made to retain vegetation within a 0.5-m radius of branches of preferred shrubs (e.g., tartarian honeysuckle) or trees (e.g., Colorado blue spruce) (Table 4).

SUMMARY

Avian nest densities and nest-site selection were examined in seven Minnesota farmstead shelterbelts for two years. A total of 617 nests belonging to 17 bird species was noted. Suitability of shelterbelts as nesting habitats was determined by nest densities which were greater than those reported for non-wooded habitats in the region. Choice of nesting substrate by the total avian community or by individual bird species was not random. Nests-sites were segregated among the five most common bird species based primarily on two linear combinations of 11 structural characteristics termed as "herbaceous" or "woody stem" variables. The five common bird species were positioned along a generalist-specialist continuum in selection of nest-sites using two measures of nesting breadth. Measures of nesting overlap varied considerably between pairs of species.

Farmstead shelterbelts, despite their small size, are important nesting habitats for birds. These "wooded islands" are sufficiently heterogenous to permit the coexistence of several nesting species at high densities. Information about nest-site choice should be used by designers of shelterbelts for the benefit of certain breeding birds in the midwest.

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